



Exploring the synergistic effects of arbuscular mycorrhiza fungi on plant development under abiotic stress

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Abstract

Plant growths and their productivity are often hindered by abiotic stresses. Crop productivity and the ecosystem are suffering due to climate change and harmful farming practices. We urgently need to use environment-friendly techniques like Arbuscular Mycorrhizal Fungi (AMF) to improve crop productivity. Generally it has been well-established that AMF are effective bio-fertilizers. It is believed that AMF injections can increase plant resilience to stressors like heat, metals, salt, drought, and extreme temperatures. AMF aids in enhancing tolerance mechanisms and safeguarding essential pathways of metabolism. AMF, as root symbionts, found within the soil give plants important nutrients (particularly inorganic), helping them grow better, produce more, and acclimatize even under stress. AMF acts as a bio-fertilizer, boosting plants' ability to adjust to different environments. Thus, researchers need to conduct further studies on how AMF promotes crop quality and productivity. This review describes the current understanding of AMF's impact on host plants at their different growth stage, their benefits, applications, and the significance of plant nutrient relationships with AMF.

Key words: AMF-plant symbiosis, Stress-tolerance, Plant-growth, Abiotic-factors, Rhizosphere, Mineral utilization, Mycorrhiza application

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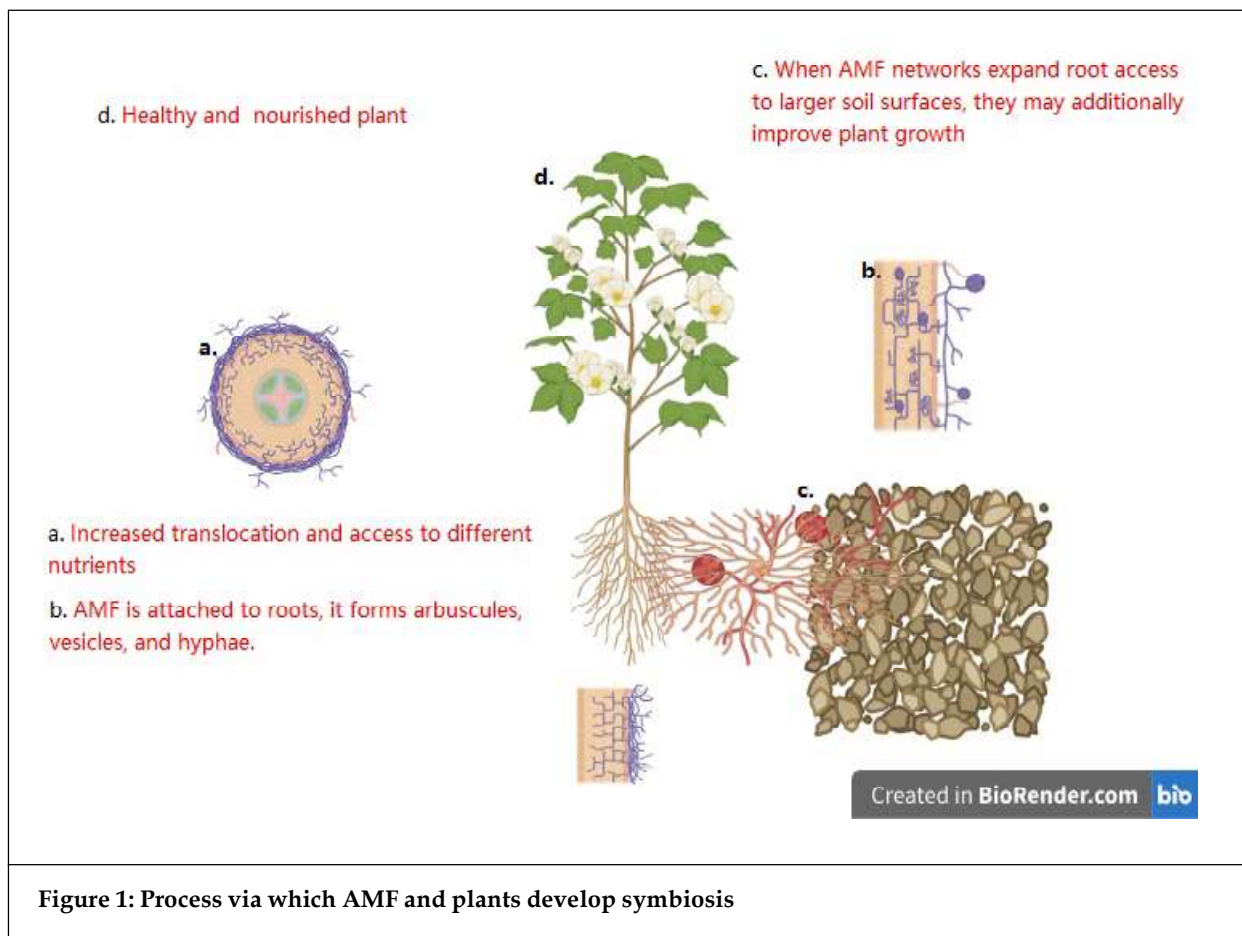
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1. Introduction

Friendly symbiotic communication between arbuscular mycorrhizal fungi (AMF) aids in growing plant crop under stressful conditions (Orine *et al.*, 2022, Bhantana *et al.*, 2021, Zou *et al.*, 2023). AMF act as facilitators in the plant host, resulting into enhanced photosynthetic activities, plant development, and prolific gaseous exchange ability in plants (Birhane *et al.*, 2012, Sun *et al.*, 2013, Yang *et al.*, 2021). It has been shown to promote adaptation to some stressful conditions which includes salinity-stress, drought-stress, heavy-metal-contamination, acidic and alkaline stress, temperature stress, and diseases are as a result of fungal-plant symbiotic relationships (Rodriguez *et al.*, 2008; Sun *et al.*, 2013, Ahanger *et al.*, 2014; Salam *et al.*, 2017, Zou *et al.*, 2023). Symbiotic relationships with AMF can be formed between over 90% of most plant species, which

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includes ferns, legumes, tubers, bryophytes, and plants that are flowering (Zhu *et al.*, 2010a; Ahanger *et al.*, 2014). When AMF is attached to roots, it forms arbuscules, vesicles, and hyphae; when it is free-living in the root system, it stays spores and hyphae. When AMF networks expand root access to larger soil surfaces, they may additionally improve plant growth (Bowles *et al.*, 2016; Yang *et al.*, 2021; Orine *et al.*, 2022). Increased translocation and access to different nutrients (nourishment uptake occurs directly via transporters, which is located and occur within the root epidermis and root hair; nourishment are moved indirectly using fungal transporter systems that activate in the extra-radical mycelium (ERM) associated with the maturing fungus before being transferred to the intra-radical mycelium (IRM) in arbuscular mycorrhizal connections or the hartig net in EM interactions (Rouphael *et al.*, 2015; Yang *et al.*, 2021) (Figure 1) are additional mechanisms that AMF can improve nutritional activity in plants.



Plant health is eventually promoted by AMF's influence on the structural and textural status of the soil (Sun *et al.*, 2013; Zou *et al.*, 2016; Thirkell *et al.*, 2017; Yang *et al.*, 2021; Orine *et al.*, 2022). AMF fungal formed hyphae contribute to the soil's increased nutrient content by hastening the break-down of organic materials (Paterson *et al.*, 2016; Yang *et al.*, 2021; Bhandana *et al.*, 2021). By promoting flow from the tips of the roots to the main roots, mycorrhizal fungi can affect how CO₂ is fixed in plants. These mushrooms offer amazing and practical advantages to all kinds of plants. It is a widely and well established fact that AMF-fungi improves nutrient uptakes, especially of phosphorus, and biomass accumulation of several crops in soils having very low phosphorus levels. AM-fungi support plants in thriving in harsh conditions. The majority of publications point out that mycorrhizal inoculation promotes plant development in soil contaminated with metals. Whether you plant flowers, veggies, trees, your plants will look noticeably better after adding them to the soil. Both indoor and outdoor plants benefit equally from the treatment, and its effects build up over time (Buckling *et al.*, 2012; Zou *et al.*, 2023).

This review iterates on the application of AMF as biofertilizers for plant husbandry, their part and function as regulators of plant development and growth, and the processes by which they are able to improve plant growth under stressful conditions and mitigate nutrient's intake.

2. History of arbuscular Mycorrhizal fungi

AMF is a natural soil resident bacteria that improves plant nutrient uptake and stress tolerance (Sun et al., 2013; Sun et al., 2018). Maturing species of AMF belong to subphylum Glocomycota, phylum Myxomycota (Spatafora et al., 2016). AMF is divided into four orders and 25 rubrics: Videlicetales, Glomerales, Paleosporeales, Paraglomerales, and Hypomorphiae (Redecker et al., 2013). Living as obligate bio-trophs they feed on stored plant products (photosynthetic) and lipids (Bago et al., 2000; Sun et al., 2013; Jiang et al., 2017).

AMF promotes plant growths by perfecting the infiltration of soil water, substrates and also available nutrients from the soils and protecting against fungal pathogens. These are important endo-symbionts because they help business growth and maintain healthy ecosystems. They play highly important role in achieving sustainable crop improvements (Gianinazzi et al., 2010; Bhantana et al., 2021).

2.1. The process of Mycorrhizae colonization in plants

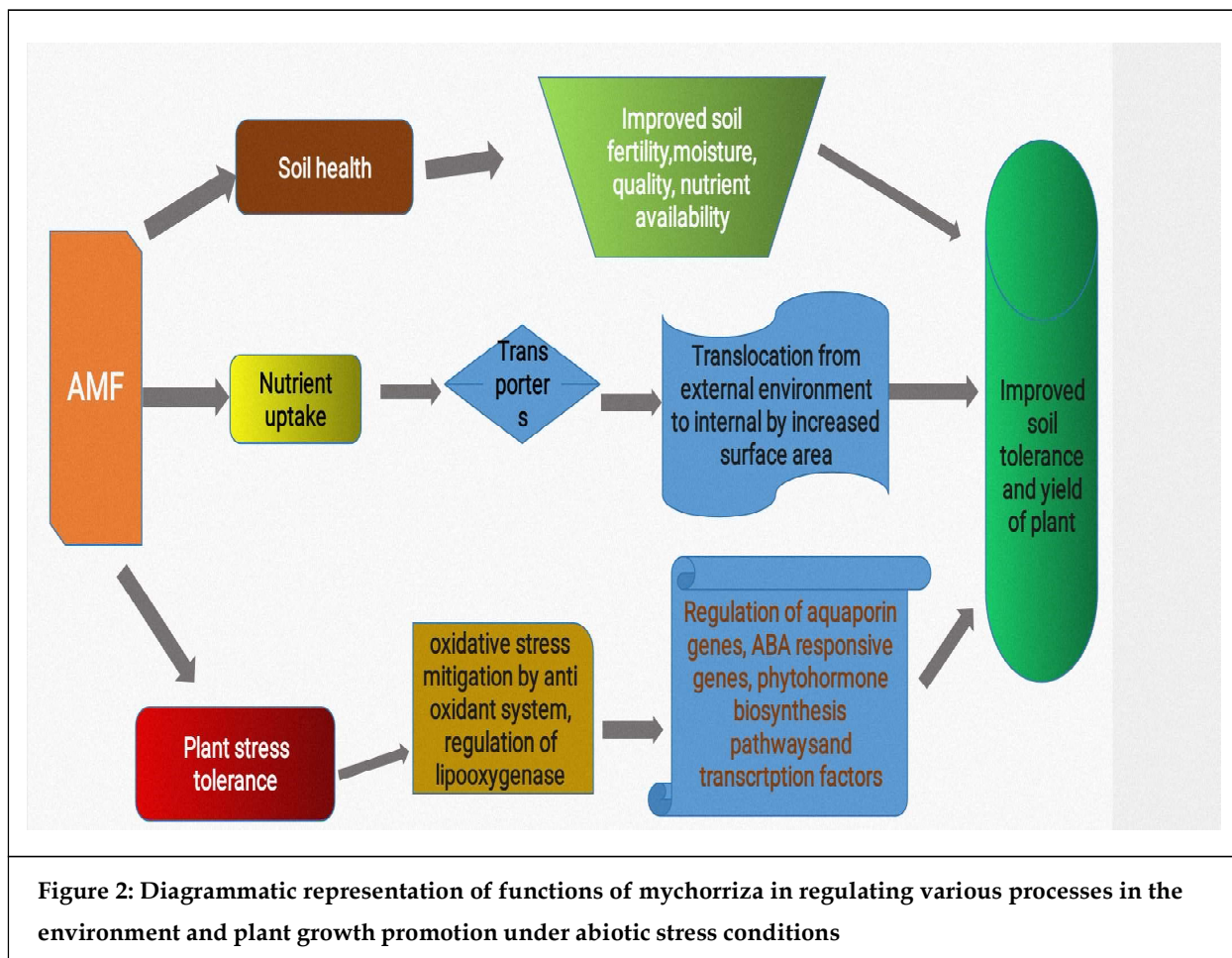
The development of these fungi on plants occurs through three main pathways: spores, colonized root fragments, or vegetative hyphae. Propagules is the term used for the latter two sources. Propagules are typically the main unit of measurement for mycorrhizae products on the label. The availability of mycorrhizae fungi near the plant's roots is a prerequisite. Exudates are fluids formed from plant's root(s) as they extend directly into the surrounding soil. Upon sensing the presence of these fluids, the nearby fungi start advancing towards the roots.

Once they arrive, they feed on the exudates and establish a colony. The root thrive by feeding the fungi, while the fungi grows along with the plant's root system. The mutual relationship continues and is strengthened as the mycorrhizae expands within the root system. Most Potting soil/compost mixes and other composed soil blends contain little or no mycorrhizae, but can be added before or during planting. Once the fungi is introduced there is quick colonization which can be hastened between AMF and plants by mixing it into surrounding soils, adding it during transplanting by wetting the seedlings or using it to coat seed before planting (Buckling et al., 2012).

2.2. The traits of AMF symbiosis

For 400 million years (Selosse et al., 2015; Bhantana et al., 2021), it is widely known for a fact that AMF-plants associations have a highly beneficial relationship. The establishment of such links occur as stepwise series of biological procedures, leading to highly beneficial effects within natural agricultural soil ecosystems (Sun et al., 2013; Van der Heijden et al., 2015). These symbiotic associations with AMF helps with regulating the growths and developments of plants within the ecosystem. Mycelial networks formed by fungi extend beneath the root structures of the plant and promoting nutrient uptakes which are sometimes unavailable. Common mycorrhizal network (CMN) can be formed by fungal mycelium which colonize the root systems of several plants, from different species. The term CMN can be described as the fundamental components within a terrestrial eco-system having major effects on the various plant communities, even in invasive plant(s) (Pringle et al., 2009) with a well-developed fungal-enhanced transportation of nitrogen (N) and phosphorus (P) plant(s) (Yang et al., 2021). In addition, rhizospheric nutrients are transferred from AMF fungi to the roots of plants, giving rise to other associated effects, allowing AMF to improve plants tolerance in response(s) to biotic and abiotic factor(s) (Plassard and Dell, 2010; Sun et al., 2013; Yang et al., 2021). AMF's are also able to boost the character of soil encouraging enhanced plant development, improves their tolerance and elevate the morpho-physiological trait(s) of plant(s) under regular and also in stressful environmental conditions or surroundings (Alqarawi et al., 2014a and 2014b, Hashem et al., 2015). The community of the terrestrial flora depend solely on AMFs as natural growth regulators. Using AMF as bio-inoculant(s) is endorsed by researchers as a relevant bio-fertilizer for sustained crop productivity (Barrow, 2012; Navarro et al., 2014). Syamsiyah et al. (2018) showed that soils when treated using AMF produce a constant mass with much higher extra-radical hyphal mycelium when compared with non-AMF treated soil(s). AMF glomalin-related protein(s) (GRSP) found in the soil is believed to regulate water contents in soil(s) experiencing or subjected to various abiotic stress types (Wu et al., 2014; Navarro et al., 2014; Orine et al., 2022), they regulate water movements between the soil(s) and plant(s), and promote plant development(s). Glomalin with other closely associated compounds protects the soil from undergoing desiccation as it enhances water-holding-capacities in the soils (Sharma et al., 2017; Zou et al., 2023). Other growth-related function(s), leaf water potential, such as the stomatal conductances, relative water contents (RWC), CO₂ assimilation and PSII efficiency are strongly impacted by AMF inoculations (He et

al., 2017; Yang *et al.*, 2021). When above-ground organs and tissues are altered, AMF can aid in improving tolerance to water stress (Bárzana *et al.*, 2015; Chandrasekaran *et al.*, 2019). With AMF inoculations, accumulations of dry-matter and water uptake(s) are enhanced, improving plant's levels of tolerance to stress conditions like salinity and also drought. Organic farm practises for growth promotion(s) with yield maximization(s) could greatly profit from utilizing AMF to promote plant growths in various biological ecosystem(s) (Figure 2).



3. AMF and plant development

3.1. AMF and mineral nutrient utilization

Excessive and uncensored land-use has left deadly impact(s) on its total bio-diversity, affecting the normal functioning within the ecosystem (Smith and Read, 1997; Balliu *et al.*, 2015; Wagg *et al.*, 2015; Jiang *et al.*, 2017). The transfers of nutrients (major and minor) is a primary role of the AMF-Plant symbiotic relationship (Nouri *et al.*, 2015; Luginbuehl *et al.*, 2017). AMF colonizations are mostly believed to be important in the process(es) of uptake of nutrients in plant(s). Inoculation of AMF has proven severally to boost the concentrations of macro and micro-nutrient(s) substantially, leads to increase(s) in the production(s) of photosynthate and increase(d) plant weight and biomass (Chen *et al.*, 2017; Mitra *et al.*, 2019). AMFs are able to increase uptake(s) of inorganic nutrient in most plant types, particularly phosphorus (Smith *et al.*, 2003; Nell *et al.*, 2010; Jiang *et al.*, 2017). Plants are able to receive more nutrients from nutrient-depleted soils when AMFs are present (Kayama and Yamanaka, 2014). Plant-AMF associations enhances phyto-availability of micronutrient(s) including copper and zinc (Smith and Read, 1997), while the absorbing capacity of host roots is increased by AMF (Bisleski, 1973). AMF-tomato association resulted in increased leaf total areas, nitrogen, calcium, potassium, and also phosphorus content, indicating boosted plant's growth rates (Balliu *et al.*, 2015; Li *et al.*, 2016). AMF's symbiotic association with root(s) allow for increased availability of essential nutrient(s) to the host plant(s) and ultimately providing mineral nutrient(s) in return, like, N, Ca, K, Zn, P and S. They are able to give nutritional supports for plant(s) under poor condition(s) within the root cell(s). AMF produces fungal-like structures known as

arbuscules, that assists in the exchange process for inorganic mineral(s) and compound(s) of phosphorus carbon etc., ultimately with an impart of considerable vigour to host plant(s) (Chen et al., 2017; Prasad et al., 2017; Bhantana et al., 2023).

Moreover, they are able to boost the phosphorus contents in the root(s) and shoot(s) system(s) (Chen et al., 2017; Al-Hmoud and Al-Momany, 2017; Orine et al., 2022), even with limited phosphorus, the mycorrhizal association(s) enhances the supply of phosphorus to the colonized root(s) of host plant(s) (Bucher, 2007; Chen et al., 2017). The Pi uptake rate(s) in maize plants colonized with AMF showed a significant improvement (Garcés-Ruiz et al., 2017). Enhanced activities (especially photosynthetic) and several leaf function(s) have been shown to occur with improvements in growth rates of the AMF inoculations that is laterally connected to the uptake(s) of P, N, and also carbon, that migrate toward(s) root(s) and promoting the developing tuber(s). It has been shown that AMF maintains P and N uptake(s) mainly by helping with plant's developments at high and low P level(s) using different irrigation methods (Liu et al., 2014; Chen et al., 2017; Liu et al., 2018). *Pelargonium graveolens* L. under limited water stress also showed increased nitrogen, phosphorus, and iron concentrations with mycorrhizal symbiosis, while Pistachio plants inoculated with AMF had higher levels of P, Zn, K and also Mn with drought related stress(es) (Bagheri et al., 2012). The Gomez-Bellot et al. (2015) study showed increased P, K and Ca levels in *Euonymus japonica* under salt related stress when AMF was present. In addition, AMF inoculation was able to improve P and N content(s) in the plant *Chrysanthemum morifolium* cell tissue(s) (Wang et al., 2018) with higher seedlings weight(s) as a result of improved water-contents and also P found intercellulaly, CO₂, and also N content(s) in *Leymus chinensis* (Jixiang et al., 2017).

3.2. AMF use bio-fertilizers

Bio-fertilizer(s) are a natural mixture used to enhance soil fertility they are beneficial for soil- health for growth and development of plants (Sadhana, 2014). Two decades, of research studies have iterated the numerous benefits that AMF gives for soil-health and also crop production. AMF may be the future key to replacing inorganic fertilizers effectively decreasing the amount of chemical fertilizers needed and released into the environment (Ortas, 2012). AMF are able to stimulate reduction of root biomass in plants while enhancing increased nutrient uptake using a larger surface area and extending deeply into the pores of the soil. The persistent use of chemicals in farm practises has given rise to several problems for soil, plants, and human health. AMF can help to reduce chemical fertilizer use by as much as 50% giving rise to better eco-friendly farm practises, this may depend on the different types of plant species and stress/environmental conditions.

4. Stress due to both abiotic and biotic factors

4.1. Drought

Stress from lack of water impedes plant life in several way(s); for example, restricted water to plant root(s) decreases the rate at which transpiration occurs inducing oxidative stress (Impa et al., 2012; Sun et al., 2013; Hasanuzzaman et al., 2013; Zou et al., 2023). Stress leaves a damaging effect(s) on drought affected plant(s) affecting the enzymatic activities, ion uptakes, and also nutrient assimilations (Ahanger and Agarwal, 2017; Jixiang et al., 2017; Ahanger et al., 2017a). Strong evidences have been shown of drought-stress alleviations with AMF applied in varied crops like wheat, soybean, barley, strawberries, maize-crop and also onion (Mena-Violante et al., 2006; Jixiang et al., 2017; Yooyongwech et al., 2016; Moradtalab et al., 2019; Zou et al., 2023). Plants ability to tolerate drought maybe as a result of the large volumes of soil exploration by associations of roots-extra-radical hyphae of the fungi (Orfanoudakis et al., 2010; Gianinazzi et al., 2010; Ruiz-Lozano et al., 2015; Gutjahr and Paszkowski, 2013; Zhang et al., 2016; Yang et al., 2021; Zou et al., 2023).

This kind of symbiosis and association(s) are believed and have shown abilities to control diverse plants and physio-biochemical processe(s) which include increased osmotic adjustments (Kubikova et al., 2001; Orine et al., 2022; Zou et al., 2023), regulating the stomata through controlled ABA metabolism(s) (Duan et al., 1996), promoted accumulations of prolines (Ruiz-Sánchez et al., 2010; Gianinazzi et al., 2010; Sun et al., 2013; Yooyongwech et al., 2013), or enhanced glutathione levels (Rani, 2016). The mutualistic relationships of varied plants with AMF amilerates for improved efficiency and root sizes, biomass and leaf-area indexes under drastic drought (Al-Karaki et al., 2004; Ludwig-Müller, 2010; Gholamhoseini et al., 2013; Orine et al., 2022; Zou et al., 2023), showing that AMF interactions with plant(s) can enable them cope with adverse environmental conditions (Ruiz-Lozano, 2003). Moreso, Morte et al. (2000) and Mena-violante et al. (2006) report that AMF symbiosis result(s) in enhanced gaseous exchange, retention of water in leaf, transpiration rate and stomatal

conductance. Recent research has indicated that ABA responses are helpful in liquid conduction through the stomata and similar physiologically related processes (Ludwig-Müller, 2010). In addition, Li et al. (2019) found that the anti-oxidant system is elevated in *Hemarthria altissima* and *Leymus chinensis* plant species, resulting in enhanced growth and photosynthesis.

4.2. Salinity

Saline-soils are a major environmental problem that pose serious threats to global food security. Salinity related-stress cause reduced plant growth via impacting vegetative development(s) and net rate(s) of assimilation, which result in lower yield and productivity (Hasanuzzaman et al., 2013; Talaat and Shawky, 2014; Ahanger et al., 2017a) and reactive oxygen species are also formed (Ahmad et al., 2010; Ahanger et al., 2017b). Several investigations are currently being done for the discovery of suitable ways to promote crop production in soils that are affected by salt to ameliorate the negative impacts, by using AMF with caution (Ahanger et al., 2018; Santander et al., 2019). According to research reports (Abdel Latef and Chaoping, 2014; Talaat and Shawky, 2014; Ahanger et al., 2018), AMF is effectively improving the growths and yields of plants subjected to salinity stress. In the findings of El-Nashar (2017) *Antirrhinum majus* plants have experienced improvements in leaf-water potential, growth-rate and water-use efficiency. Some physiological characteristics such as photosynthetic rates, conductance in the stomata, and leaf water retentions can benefit from AMF symbiosis with plants that are cultivated under saline conditions. Mycorrhizal had a significant effect in alleviating the adverse impacts of salinity conditions on photosynthesis (Sheng et al., 2011). AMF inoculation was effective in improving the photosynthesis rate, other gas exchanges, leaf chlorophyll contents, and water-use efficiencies of *Ocimum basilicum* L. when under high salinity. The growth traits of *Allium sativum* plants, such as the index of the leaf-area and plant biomass, have improved in salinity conditions in the past (Borde et al., 2010). Under moderate saline condition(s), mycorrhiza inoculations led to an impressive increase(s) in fresh and also dry weight(s), as well as an increase in nitrogen concentration in shoot and root, as determined by Wang et al. (2018).

4.3. High and low temperatures

AMF interactions greatly influences plant rhizospheric responses with changes such as increasing soil temperatures, leading to positive yield and production increase which are sustainable (Bunn et al., 2009; Sun et al., 2013; Yang et al., 2021). Heat related stress have significant effects on plant growths and also developments, their influences include i) losing plant's vigor in addition to inhibiting time of seed-germinations, ii) retarding plant growth-rates, iii) decreasing biomass values, iv) leaf and reproductive organs wilts and burns, v) abscising and senescencing of plant leaf, vi) spoilage and loss of fruit colour, vii) yield reduction and cell deaths (Wahid et al., 2007; Bunn et al., 2009; Hasanuzzaman et al., 2013) and viii) elevated oxidative stress(es). AMF-inoculated plants generally grow better when subjected to heat stress (Gavito et al., 2005; Sun et al., 2013; Yang et al., 2021). The study by Maya and Matsubara (2013) report the close association(s) of AMF (*Glomus fasciculatum*) in plant(s) leads to positive change(s) in growths and yields under the higher temperatures (Figure 3).

Photosynthesis is well documented as a highly sensitive to temperature stress and is usually first affected and then other related symptoms of stress become visible (Berry and Björkman, 1980). When photosynthesis is limited, plant(s) growth is reduced under lower or higher temperature(s) (Wahid et al., 2007), with AMF, stimulation of photosynthetic performances that are different from the non-AMF plants that are visibly expressed (Augé 2001; Zhu et al., 2011). Temperature related stress in AMF inoculated plants show higher Pn than in non-AMF plant crops (Ruotsalainen and Kytöviita 2004; Wahid et al., 2007; Zhu et al. 2010a; 2016), having more capacity to assimilate CO₂. However, Wu and Zou (2010) report no impact with AM inoculation on Pn in Citrus (tangerine) seedlings when grown at low temperatures. Stress leads to decreased chlorophyll concentrations, because chlorophyll biosynthesis is adversely affected or increased chlorophyll degradation rates, as reported by many authors. The work of Paradis et al. (1995), report higher chlorophyll concentrations in AMF inoculated plants than plants without AMF at regular temperatures, showing that temperature related stress rarely interferes or tampers with light-harvesting and chlorophyll-synthesis in AMF and alleviating damages to mesophylls chloroplasts, improving photosynthetic-efficiency than in non-AMF plants (Evelin et al., 2009). On the contrary, the study of Charest et al. (1993) report that AMF-maize plant(s) produced lower chlorophyll concentrations, but more carotenoid content. AMF take crucial role to protect the photosynthetic apparatus acting as aids to light harvesting pigments (Young et al.). Zhu et al. (2011) also observed AMF- maize plant(s) had more carotenoid concentrations than the plants having no AMF showing that AMF colonization

helps with stabilizing the lipid related phase(s) within the thylakoid membrane(s), providing photo-protections for cell structure(s) and also photosynthetic related apparatus(es) (Karim *et al.* 1999; Wahid *et al.*, 2007; Orine *et al.*, 2022; Zou *et al.*, 2023).

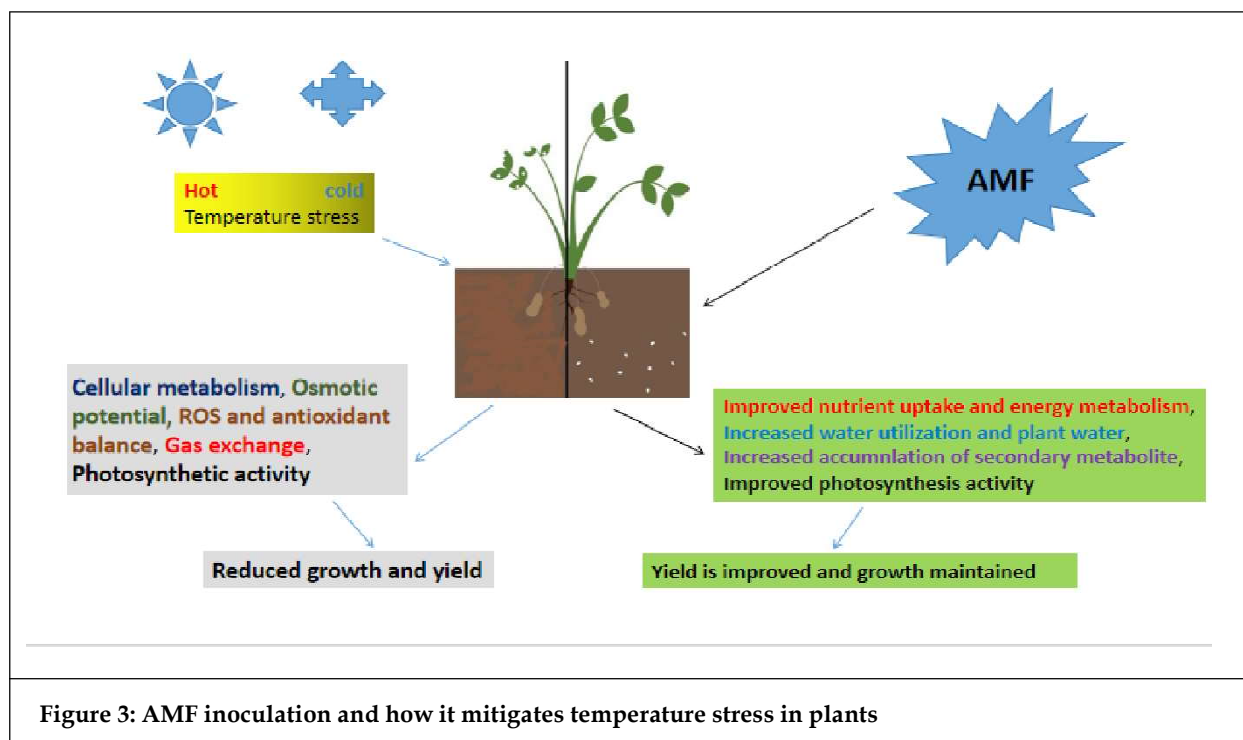


Figure 3: AMF inoculation and how it mitigates temperature stress in plants

AMF increases plant ability for tolerance under cold temperatures (Birhane *et al.*, 2012; Chen *et al.*, 2013; Liu *et al.*, 2013; Yang *et al.*, 2021), giving rise to better growths than in non-AMF experimental plants (Abdel Latef and Chaoxing, 2011b; Sun *et al.*, 2013; Chen *et al.*, 2013; Liu *et al.*, 2013; Yang *et al.*, 2021). AMF supported plants are able to easily combat cold stress, resulting in eventually improved plant developments (Gamalero *et al.*, 2009; Birhane *et al.*, 2012; Zou *et al.*, 2023). In addition, AMF helps with the retention of moisture inside its host-plant (Zhu *et al.*, 2010a), increasing secondary produced metabolites that strengthens the plant's natural immunity system, enhancing water-conservation capacity and water-use efficiency (Zhu *et al.*, 2010b) and increases protein contents aiding the plants to combat cold environments (Abdel Latef and Chaoxing, 2011b) (Figure 3). AMF Symbiotic relationships forges good water-plant relationship(s) and osmotic adjustments (Zhu *et al.*, 2012; Zou *et al.*, 2023). AMF promotes the process of synthesizing chlorophyll with significant improvements in metabolite(s) concentration(s) in plant(s) growing under cold stress condition(s) (Zhu *et al.*, 2010a; Sun *et al.*, 2013; Yang *et al.*, 2021). AMF also helped in altering protein contents in tomato(es) and other vegetable(s) subjected to cold-stressed environments (Abdel Latef and Chaoxing, 2011b).

At increasing higher temperatures (HT) deleterious effects on plant growth were noticed but the protective and helpful role(s) of Arbuscular mycorrhizal fungi (AMF) when plant(s) were cultivated under stress conditions, were particularly able to enable the experimental plant(s) to survive (Mohammadi *et al.*, 2011). Under high-temperature pepper inoculated with *Glomus* isolate and *G. intraradices* mixtures had enhanced growths relative to non-AM controls, in spite of the reduction in amounts of AM colonization showing lesser transferred fungal P to the plants (Martin and Stutz, 2004).

4.4. Heavy metals

AMF are commonly believed to assist plant to establish themselves in soils with heavy-metals contaminants, as they have the potentials to strengthen the defence systems of the AMF colonized plants promoting growths and also development(s). Accumulations of heavy-metal(s) in staple food crops, fruits, veggies, and soils lead to several health hazard(s) (Liu *et al.*, 2013; Yousaf *et al.*, 2016). Aguilera *et al.* (2014) revealed that AMF association(s) with wheat significantly increases nutrient uptakes when subjected to aluminum stress. While shoot-root growth(s), leaf and cell death in crops planted on soil(s) enriched with Zn and Cd were highly suppressed (Moghadam, 2016) as also seen in repeated studies which have explored the effects of AMFs on

metal-accumulation in plant(s) (Souza *et al.*, 2012). The heavy metal(s) deactivated in the fungal hyphae (both external and internal types) (Ouziad *et al.*, 2005), which are able to collect and fix such heavy metals within their cell walls to be stored within vacuoles or chelated along with other substance(s) that immobilizes them inside the cell cytoplasmic walls (Punamiya *et al.*, 2010) significantly reducing the plants metal-toxicity. AMF are highly effective on plant developments and growths especially in stress-induced conditions and aids in increasing the physiological and morphological processes which enhance plant(s) biomass (root and shoot) and uptakes of immobilized nutrient(s) including Zn, Cu and P ultimately reducing the metal toxicity in plant(s) under these harsh condition(s) (Kanwal *et al.*, 2015; Miransari, 2017). Additionally, metal dilution in plant tissues may result from increase(d) growths or chelations within the rhizosphere (Kapoor *et al.*, 2013; Sun *et al.*, 2013; Audet, 2014; Bhantana *et al.*, 2021). According to the study by Andrade and Silveira (2008) and Garg and Chandel (2012), AMF is said to bind Zn and Cd within the cell wall(s) of mantle hyphae and of cortical cells, limiting uptakes and improving yield, growth, and nutritional status.

Numerous metals that plants acquire from within the rhizosphere are carried through the root zone(s) to aerial portions of the plant can be interrupted by mycorrhizae (Dong *et al.*, 2008; Kapoor *et al.*, 2013; Li *et al.*, 2015). For mycelial of various AMFs, there is a high metal absorption and cation-exchange capacities (Takács and Vörös, 2003). As demonstrated in *Lolium perenne* found in severely contaminated soils with varying contaminants such as Ni, Cd, and Zn, metals, the presence of non-adapted AMF fixes the pollution within soil(s) and reduces uptake and accumulations of heavy metals (Takács and Vörös, 2003). It is believed that AMF regulates the absorption and build-up of a few essential inorganic nutrients.

There have been reports of elevated uptake of Si in plants with mycorrhiza, such as *Glycine max* and *Zea mays* (Yost and Fox, 1982; Clark and Zeto, 2000). According to Hammer *et al.* (2011), Si was substantially absorbed by *Rhizophagus irregularis* propagated spores and formed hyphae and then transported towards the host root. It is highly important to iterate that AMF may also be used to address inadequate Cd toxicity and mobility by increasing the pH of the soil (Shen *et al.*, 2006), supplementing Cd inside extra-radical mycelium walls (Janoušková and Pavlíková, 2010), attaching Cd to the glycoprotein glomalin. AMF was very effective in lowering rice's Cd levels, particularly in the cell walls and vacuole(s), which resulted in Cd detoxifications (Li *et al.*, 2016a).

According to the report of Wang *et al.* (2012), the altered chemical form(s) of Cd in many plant tissues could have influenced alfalfa's (*Medicago sativa* L.) increased Cd tolerance through AMF-mediated means. The AMF plays a role for a number of processes, including the immobilization and limitation of metal compound(s), the precipitations of polyphosphate granule(s) in soil, the adsorptions to the chitin of cell walls of fungi, and the chelations of heavy metal(s) inside the fungus (Figure 2).

4.5. AMF and combined abiotic stresses

It's commonly acknowledged that AMF can assist to reduce a number of stress(es) or combination(s) of stresses, including as heavy metals, temperature, salinity, nutrients, and drought. For instance, plants exposed to both salinity and drought produce more reactive oxygen species, which are sometimes extremely harmful to plant(s) (Baudh and Singh, 2012). Enzymes such as catalases (CAT), peroxidases (POD), glutathione reductases (GR) and superoxide dismutases (SOD) are extensively used in the process detoxification of the reactive oxygen species (ROS) (Ahanger and Agarwal, 2017). Moreover, tomato(es) plants with which *Sclerotinia sclerotiorum* was inoculated with exhibited enhanced biomass output, stomatal conductance, leaf water relations and Fv/Fm in comparison with the un-inoculated plants when drought and salinity were applied simultaneously (Duc *et al.*, 2018). Therefore, according to several studies (Abdel Latef, 2011; Abdel Latef and Chaoxing, 2011b; Abdel Latef and Chaoxing, 2014), AMF are essential for enhancing plant development and yield outputs under stress. There are extremely few research reports in the literature that show how AMF helps to mitigate the combined impacts of two or more stresses. Through a number of mechanisms, including enhanced photosynthetic rate, accumulation of osmoprotectants, uptakes and accumulations of mineral nutrients, up-regulation of antioxidant enzymatic activities, and changes to the rhizospheric ecosystems, AMF's symbiosis shields plants against wide ranges of abiotic stress(es) (Bárzana *et al.*, 2015; Calvo-Polanco *et al.*, 2016; Yin *et al.*, 2016). Several research (Augé *et al.*, 2014; Lehmann *et al.*, 2014; Lehmann and Rillig, 2015) have demonstrated increased nutritional qualities of AMF plant(s) when subjected to osmotic stressed-environments as a result of salinity or deficit watering. It's possible that tolerance mechanisms are similar because of coupled stress adaptations mediated by AMF. It is suggested that similar mechanisms generated by varied stresses may

include AMF-mediated change(s) in the phytohormone profiles, mineral absorptions and assimilations, build-ups of suitable secondary metabolite(s) and osmolytes, and up-regulations of antioxidant(s) system(s). Certain mechanisms, such as the formation of phytochelatin, the sequestration and compartmentation of harmful ions, and protein expression, can be unique and vary significantly depending on the type of stress and AMF species involved. Osmotic stress tolerance can be significantly enhanced by altering root characteristics such as hydraulic conductivities (Evelin *et al.*, 2009). The research of Zhang *et al.* (2018) found that via modifying gas-exchange characteristics and the concentrations of several important metabolites, the AMF insulated castor beans against saline stress. The aforementioned qualities of AMF have potentials for improving the nutraceutical quality of crops and may have substantial agronomic implications for the management and the productions of many prospective crops. To fully understand how AMF works to offset the impacts of combined, more research is necessary.

5. AMF and plant growth

5.1. Germination

Plants are often stimulated by mycorrhizal fungi to decrease biomass of roots while also increasing nutrient(s) uptake capacities by reaching far beyond the root's surfaces and multiplying in soil pores enhancing germination. In a study using two sampling periods, there was high significant differences in seed germinations rate per treatment, but not in the final sampling period. Inoculated plants that initiated flowers and pods had a higher number of inoculated plants than controls. Mycorrhizae's positive effects on plant growth can be attributed to decreased germination periods and boosted plant developments, as shown by the findings of this study. This earlier development is not known to have a physiological explanation. Plant and mycorrhizae exudates are known to have complex chemical interactions that are able to impact on the numerous aspects of plant developments. Plant strigolactones serve as signal compounds for the initial stages of Arbuscular mycorrhizae colonizations, stimulating fungal metabolism and branching, while also promoting seed germination. According to Fusconi (2014), AM is associated with an increase in the production of auxins and cytokines, which stimulate plant growth. It's unclear if these chemical interaction(s) are responsible for the earlier germinations and reproductive development(s) of rapid Growth, which necessitates more experimental scrutiny. This study suggests that adding mycorrhizae can speed up the colonizations and propagations of desired plants in a natural environments. Mycorrhizae can significantly impact habitat restoration efforts due to their ability to accelerate plant development and germination. Agriculture could be positively impacted by having shorter crop cycles. More studies may explore the effects of mycorrhizae on colonizations and propagations of desired vegetations in non-greenhouse experiments Gutowski, Valeria (2015) "The resulting effects of mycorrhizae on seed developments, germinations, and reproductive yields with rapid growth," (Binti *et al.*, 2023). The interactive resulting effects of light, mycorrhizal status and exogenous carbon, on germinations and growths were investigated in-vitro with use of axenic agar microcosms for three geophytic orchid species and one tropical epiphyte. The geophytic species strongly depend on their associated mycorrhiza for growth and cannot be replaced by exogenous sucrose, while on the other hand the epiphytic species can. Exogenous sucrose in the dark resulted in the epiphytic species achieving 95% of more mycorrhiza seedling volumes. Germination was made possible by the strong interaction between mycorrhiza status and light exposure. In the absence of mycorrhiza, light can hinder or severely reduce the growth of terrestrial orchids (Sameera, 2019). Mycorrhiza's role in the increase in phytohormones and enzyme activities supporting seed germinations and growths of orchids.

5.2. AMF and plant yield

The quality of crops is enhanced by beneficial rhizosphere microorganisms, which improve the nutrient status as described above. AMF-colonized strawberry showed an increase in secondary metabolites, which led to improved antioxidant properties (Castellanos-Morales *et al.*, 2010). AMF's ability to affect and produce carotenoids and volatile compounds can improve the dietary quality of crops (Hart *et al.*, 2015). The quality of the tomatoes was observed to be beneficial by Bona *et al.* (2017) due to the beneficial effects of AMF. Zeng *et al.* (2014) found that *Glomus versiforme* caused a rise in sugars, vitamin C, organic acids, flavonoids, and minerals, which resulted in improved citrus fruit quality. Chlorophyll, anthocyanins, carotenoids, total soluble phenolics, tocopherols and various mineral nutrient(s) are increased in mycorrhizal symbiosis, as demonstrated by Baslam *et al.* (2011). AMFs have been used for large-scaled farm cultivations of potatoes (Hijri, 2016), maize-

crop (Sabia *et al.*, 2015), and yam-crop (Lu *et al.*, 2015) demonstrating their significant potentials to increased crop yield. By enhancing the biosynthesis of important phytochemical(s) in edible plant(s), AMF can make those plants more suitable for the chain that produces healthy food (Sbrana *et al.*, 2014; Rouphael *et al.*, 2015). It has generally been suggested that maintaining the pH of the soil could help AMF mitigate abiotic stress and preserve its horticultural value (Rouphael *et al.*, 2015). Furthermore, AMF can be extremely important in enhancing plants' ability to withstand harsh conditions. Mycorrhizae on boosting production and growth in nine horticultural plants at two distinct P fertilization rates in a field setting (Ronsheim, 2012). According to Ortas (2010), the findings of the field experiment demonstrated that mycorrhiza inoculation greatly improved fruit yield and cucumber seedling survival. The studies of Gao *et al.* (2020) found a statistically significance of 28.54% increase in yields in cotton between inoculated and non-inoculated control plots.

5.3. Fight pathogens

Numerous plants associate with fungus to produce what are known as mycorrhizae, which allows the plants to obtain soil nutrients and shields them from toxins and disease. In addition, mycorrhizae aid in shielding plants from soil-borne diseases such as mold and pests. AMF can enhance the manufacturing of beneficial phytochemical(s) in edible plant(s), to make them more suitable and adapted for the chains of production of healthful food (Sbrana *et al.*, 2014; Rouphael *et al.*, 2015; Orine *et al.*, 2022; Bhandana *et al.*, 2021). According to reports, AMF may mitigate abiotic stress by maintaining the pH within the soil, preserving its horticultural values (Rouphael *et al.*, 2015). Plants that form mycorrhizae – associations with fungi retrieve nutrients from the surrounding soils and are shielded from toxins and disease. They help plants avoid being affected by bugs, mold, and harmful pathogens living in the soil.

5.4. Photosynthesis

It is known that (AM) boosts nitrogen fixation and photosynthesis in plants. Cotton with AMF symbiosis demonstrated in increased growth, photosynthesis, number of bolls for each plant, and cotton ripeness (Gao *et al.*, 2020). Given that chlorophyll molecules efficiently absorb nitrogen, the amount of chlorophyll in plants colonized by AMF rises (De Andrade *et al.*, 2015), the mycorrhiza arcs has become well known as agents that accelerate photosynthesis and nitrogen fixation in plants. Nonetheless, in cold-stressed cucumber seedlings, AM has a negligible effect on leaf chlorophyll (Bulgarelli *et al.*, 2020). AM exerts zero impact on gas exchange or PSII fluorescence in guar (*Cyamopsis tetragonoloba* (L.)). In order to produce gum, photosynthesis was boosted in legumes, namely in Bambara groundnut (El-Sawah *et al.*, 2021). This demonstrates that AMF can contribute significantly to improved photosynthesis.

5.5. Water use efficiency

Arbuscular mycorrhizal (AM) fungus modify the water interactions of plants during droughts, increasing the plants' tolerance to the dry spells. Using a randomized greenhouse experiment, Birhane *et al.* (2012) studied the impactful effects of the symbiotic relationship of plants with AM and precipitation pattern on the growth, transpiration, nutritional status, and mycorrhizal responsiveness in seedlings of *Boswellia* plants. Plants that mycorrhizal Mycorrhizal plants possess decreased rates of transpiration than non-mycorrhizal plants, which optimizes water usage efficiency.

5.6. Soil enzymatic activity

A meta-analysis of multiple research revealed that distinct AMF types impact soil enzyme activity, even though the precise magnitude of these consequences has not been reported yet. Neutral pH and lower accessible phosphorus are necessary for AMF's optimum influence on soil enzymatic activity. An increased soil enzymatic activities may result from AMF's encouragement of plant growth. The employment of AMF inoculation in agriculture has advantages. Arbuscular mycorrhizal fungi possess a positive effect on the soil enzyme activities and boost plant biomass, in accordance to findings published by Mingsen *et al.* (2019). The percentage of root colonization or plant growth proved to be associated with endoxyloglucanase activity in mycelia connected to root development in plants.

As reported by Arriagada *et al.* (2012), introducing mycorrhiza to *G. claroideum* + *T. versicolor* resulted in a substantial rise in the rate of activity of the dehydrogenase enzyme, but introducing plants with *G. claroideum* alone showed a significant boost in α -glucosidase activity in blueberries. Cellulase and xylanase activity were considerably higher in grassland orchid fungus. While the fungi from orchids with epiphytic growth favor

starch and arginine, the fungi from terrestrial orchids utilized carboxymethyl cellulose with greater efficiency. The extracellular enzyme output of fungi from grassland and epiphytic orchid species differ, according to the current research, indicating that they have become accustomed to various growing environments. In order to mitigate the harmful effects caused by temperature-stress causes to maize plants, the AM fungus could decrease the amount of lipid in membranes. Enzymes like superoxide catalase, dismutase and peroxidase appeared more active in the roots and leaves of plants after colonizations with AMF.

The investigations by Chen *et al.* (2013), Liu *et al.* (2013), and Birhane *et al.* (2012) suggests that AMF is capable of improving plant immunity to cold stress. The vast majority of research indicates that crops treated with AMF at colder temperatures grow better than plants treated without AMF (Zhu *et al.*, 2010b). AMF helps plants fight off cold stress, a process that in turn fosters optimized plant developments (Gamalero *et al.*, 2009; Birhane *et al.*, 2012; Sun *et al.*, 2013, Yang *et al.*, 2021). It also helps the plants that are being treated retain water (Zhu *et al.*, 2010a), boosts secondary metabolism in plants which boosts their immune system, and raises protein content in plants to help them fight off the cold (Abdul Latef and Chaoxing, 2011b). Improvements in the interactions between plants and water are credited to the presence of AMF associations in plants under stress (Zhu *et al.*, 2010a; Abdel Latef and Chaoxing, 2011b). Additionally, it has documented how AMF affects tomato and other vegetable protein levels when exposed to cold stress conditions (Abdel Latef and Chaoxing, 2011b). High temperatures on the other hand exerted a detrimental effects on plant growths (HT). Previous studies has proven the highly protective role of Arbicular mycorrhizal fungi (AMF) in stressful environments, (Mohammadi *et al.*, 2011).

Furthermore, AMF treated plants exhibit greater productions of salicylic acid, jasmonic acid, as well as a number of additional significant inorganic nutrients. For example, under salt-stress conditions, the AMF-treated *Cucumis sativus* plants had greater concentrations of total P, Ca²⁺, N, Mg²⁺, and K⁺ than the uninoculated plants (Hashem *et al.*, 2018). In saline conditions, mycorrhizal-inoculated *capsicum annum* exhibited greater levels of chlorophyll in leaf, as well as greater Mg²⁺ and N absorption, but poorer Na⁺ transportions (Cekic *et al.*, 2012). Furthermore, using lettuce in their work, showed that the mycorrhizal plants exhibited more biomass, improved N uptake, increased proline synthesis and obvious variations in ionic relations, notably less retention of Na⁺, than those in non-mycorrhizal plants under stressed conditions (Santander *et al.*, 2019). Crucial growth regulators can have their levels efficiently regulated by AMF inoculation. In accordance with studies by Talaat and Shawky (2014) and Hameed *et al.* (2014), AMF increases cytokinin quantity, which causes a notable photosynthetic transport during salinity stress. Growth promotion during salinity stress is triggered by an alteration in the polyamine pool, which is mediated by AMF (Kapoor *et al.*, 2013). Increased strigolactone in AMF-treated plants substantially decreased the consequences of different saline effects on lettuce plants (Aroca *et al.*, 2013). Crop colonization with AMF may minimize oxidative stress by suppressed lipid membrane peroxidations under salinity-stressed conditions (Abdel Latef and Chaoxing, 2014; Talaat and Shawky, 2014). Additionally, it was discovered that AMF inoculation accelerated the accumulations of multiple organic acids, which resulted to increases the process of osmoregulation in plants nurtured in salinity-laden conditions. Sheng *et al.* (2011), for instance, observed that maize plants planted in salty soil had higher synthesis/accumulations of certain particular organic acids, and that AMF promoted increased productions of betaine, validating what indirect roles are played by AMF in vegetative osmoregulations under salinity stressed environments.

The findings suggest that the AM fungus can mitigate the detrimental impacts of temperature stress on maize plants by limiting membrane permeability and lipid peroxidation while augmenting the build-up of osmotic equilibrium chemicals and antioxidant enzyme activity. AMF invasion in plants additionally, affects the activities of catalases, peroxidases and superoxide dismutase in plant leaves and roots have been boosted by the biofertilizer. By raising the production of the enzymes such as phosphatase, protease, dehydrogenase and invertase, treatments have enhanced soil microbial activity (El-Sawah *et al.*, 2021).

6. Conclusion and future prospects

Several investigations have previously established the beneficial impact of AMF in enhancing plant growth in stressed situations. In order to comprehend the symbiotic relationships that formed and exists between AMF and a range of plants in stressful conditions, the updates of information addressing the beneficial roles of AMF has been presented in a logical manner in this review. It recently came to light that plants to which AMF was inoculated can effectively and efficiently combat a wide range of environmental stressed situations, like

drought, salinity, cold-stress, nutrient-stress and severe temperatures. AMF have primarily been discussed as beneficial organisms for the absorption of nutrient(s) from soil which contributes to enhancing the per hectare yields of a several numerous crops (such as cereals, legumes, tubers), horticultural plants and also vegetables. Promoting the use of AMF is essential to the sustainability of contemporary global agricultural systems. It is indisputable that applying AMF to improve agriculture may assist in fostering bio-healthy agriculture through lowering the volume of synthetic fertilizers as well as other chemicals utilized. AMF-mediated crop cultivation and yield enhancement can help agricultural plants meet the world's growing population's consumption needs. Environmentally friendly technologies will become increasingly popular and highly encouraged. Subsequent investigations need to be focused on pinpointing genetic components and genetic products that drive the regulation of AMF mediated developments and growth in high-stress environments. Identification of the key physiological and also the metabolic pathways when under various environmental conditions, as well as specific plant hosts and AMF specific protein factors controlling symbiotic interaction, can be highly interesting for future researches. Understanding the modifications that AMF causes in the tolerance methods, mechanisms and the communication between them that is set off to control plant performance can help to increase crop productivities. AMF activities needs to be researched at all levels in order to investigate its function in natural environments as bio-fertilizer(s) for sustainable agricultural output.

Proteomics strategies may be significance in expanding the comprehension of the molecular foundations of AMF plant resistance to temperature-stressed conditions and for managing it. Across nature, AMF fungus can be found; they aren't restricted to their host plants. Nevertheless, temperature-stressed circumstances determine how successful AM symbiosis is. In order to inoculate plants that are acclimated to temperature-stress, it is highly necessary that future studies evaluate isolates of native and potential temperature-stress-tolerant AMF species. A significant consideration is the current situation of the global climate. The change scenarios anticipate that temperatures will climb and that extreme temperatures may occur more frequently, heightening the likelihood that crops will be exposed to unfavorable temperatures. Multiple investigations have shown that this strategy works better for agriculture in the future than trying to adjust to unfavorable environmental conditions. There are still difficulties with AM application in agriculture, such as the need to cultivate AM fungi on a big scale and intense competition from other micro-organisms in the soil environments.

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